

Fragmentation, disturbance and tree diversity conservation in tropical montane forests

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Summary

1. Loss in forest cover associated with human activities leads to forest islands within a fragmented landscape. Anthropogenic disturbance may also directly alter tree species diversity. Habitat fragmentation and disturbance may have implications for biodiversity conservation and can affect a variety of population and community processes over a range of temporal and spatial scales. Effects are manifest both within and between fragments. The complexity of this process challenges the predictive value of simple models based on island biogeographical theory.

2. We analysed data on tree species diversity from 195 field plots in 16 tropical montane forest fragments in the Highlands of Chiapas, Mexico. Within this area we identified five community types. Variation in species diversity between fragments in each community was analysed by fitting linear models in which area, core area, edge/area ratio, and mean proximity index were related to mean plot diversity. Variations within fragments were then analysed using linear mixed-effects models in which the fixed effects were considered to be proximity to edge, canopy closure and a degradation index, whereas fragment-level variation was modelled as a random effect.

3. Effects of fragmentation *per se*, defined as the reduction in area and connectivity between fragments, were not detectable. Within-fragment effects, however, were evident. Disturbance was associated with lower tree diversity at a local scale, and a notable impact on late successional species.

4. While not statistically detectable, we expected fragmentation *per se* to be acting to reduce diversity in the long term. We therefore complemented our analysis by calculating the theoretical loss in species when the number of tree stems in a fragment was halved for each community type using resampled accumulation curves. These models predicted a maximum loss in transitional forest (12 species lost) and evergreen cloud forest fragments (seven to nine species lost) and a minimum loss in oak forest fragments (three species lost).

5. Synthesis and applications. Our results call into question the utility of island theory when setting conservation priorities for tree species. In our study region, and elsewhere, tree diversity is most immediately threatened by the effects of within-fragment disturbance. The few remaining areas of intact native forests should be prioritized for conservation regardless of their size and connectivity. If diversity is conserved within these fragments, the short-term effects of landscape-scale change may be minimized. They may then be reversed if long-term restoration initiatives can be implemented.

Key-words: disturbance, fragmentation, island biogeography, linear mixed-effects models, species accumulation curves, species loss, tree diversity

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Introduction

Historical and contemporary losses in forest cover associated with human activities occur in many regions of the world, particularly in tropical regions (Rudel & Roper 1997; Lamb, Erskine & Parrotta 2005). Extensive deforestation leads to forest islands within a fragmented landscape. In addition, forest fragments can be selectively logged, degraded by ground fires and overhunted. These local disturbances alter the ecological processes operating in the fragments and may have additive or interactive effects with fragmentation on forest community structure and function (Cochrane *et al.* 1999; Nepstad *et al.* 1999; Gascon, Williamson & Fonseca 2000; Laurance & Cochrane 2001).

Habitat fragmentation and disturbance may have implications for biodiversity conservation and can affect a variety of population and community processes over a range of temporal and spatial scales (Saunders, Hobbs & Margules 1991; Debinski & Holt 2000; Fahrig 2003). However, separating the effects of each causal process can be challenging because (i) the effects of 'habitat fragmentation' often co-vary with the effects of local 'human disturbance' (Villard, Trzcinski & Merriam 1999; Caley, Buckley & Jones 2001; Haila 2002) and (ii) different organisms and ecosystems may experience the degree of fragmentation and disturbance in variable, even contradictory, ways (Haila 2002; Henle *et al.* 2004).

To link observations with underlying theory (MacArthur & Wilson 1967 and the extensive literature flowing from it), many studies on species diversity draw analogies between forest fragments and oceanic islands (Harris 1984; Laurance & Bierregaard 1997; Rosenblatt *et al.* 1999; Ferraz *et al.* 2003; Hill & Curran 2003). However, the island theory has some basic simplifying assumptions that may be not relevant to many actual situations (Gotelli & Graves 1996). For example, (i) fragments exist within a complex vegetation matrix making isolation distance difficult to measure; (ii) the degree of isolation varies across key processes, including dispersal and the extent of natural disturbances; (iii) the time scale of human-induced fragmentation is rarely long enough for tree populations to reach equilibrium levels; (iv) climate and soil usually vary at a regional scale, making direct comparisons between forest fragments difficult; (v) within-fragment processes can be more important in their effects on species diversity than landscape-scale processes; and (vi) too few individual fragments may be found/sampled in a given landscape to allow a statistically rigorous test of theory.

In this study we evaluated the effects of fragmentation as a result of regional deforestation and the effects of local, more subtle, habitat disturbances on tree species diversity. We defined fragmentation effects *per se* as those that directly reduce the pool of species at the fragment level through reduction in area and connectivity. These effects can have both historical and recent origin. Recent fragmentation is the result of human-induced

isolation of areas of natural forest in a landscape. We defined local effects as those associated with anthropogenic actions that could also lead to fragmentation *per se* but that did not necessarily reduce either the size or the connectivity of the fragments. An increase in edge effects or internal disturbance are all local effects manifest within fragments. In practice it is difficult, if not impossible, to separate cleanly both types of effects. However, we structured our data analysis in such a manner that the relative detectability of each of these sets of effects could be drawn out. This allowed us to interpret our case study as an empirical test of the practical utility of island theory for conservation of tree species diversity in a fragmented forest landscape.

Some of the questions that motivated this study were as follows. (i) At what scale are the complex effects of forest fragmentation detectable? (ii) Does the detectability and strength of the relationships differ between forest types? (iii) Does the strength of these effects vary between fragments within each forest type? (iv) Is the response different between late successional and pioneer tree species? (v) How many species would we expect to lose for each forest type if the number of individuals in a fragment was halved? To answer these questions we estimated the relative importance of variables that were hypothesized to influence tree diversity at different scales. These were (i) climatic gradients operating at a landscape scale, (ii) fragmentation effects *per se* operating at the fragment scale (between-fragment effects) and (iii) effects of fragmentation and habitat disturbance operating at a local scale (within-fragment effects). Additionally, we asked if there were differential responses of tree species guilds (late successional and pioneer species) to these factors. Finally, we predicted the potential loss of species associated with continued deforestation, for which we used resampled species accumulation curves for the various forest fragments. By analysing the complex determinants of species diversity, including landscape and local processes, this study provides better insight into how to address the conservation of tropical montane forests.

Methods

STUDY AREA

The study was conducted in the Highlands of Chiapas (Fig. 1), south-eastern Mexico. The Highlands of Chiapas is a biologically diverse region extending over 11 000 km², which includes 30% of the about 9000 vascular plant species of the flora of Chiapas (Breedlove 1986). It comprises a mass of high altitude land (> 1500 m a.s.l.). The soils include thin lithic rendzinas and rather infertile chromic luvisols. The climate is cool (mean temperatures ranges between 14 °C and 17 °C) and humid (annual rainfall ranges between 1200 and 1800 mm), with a rainy summer and 5–6 month dry season. Several forest types are found in the region, including oak, pine–oak, pine and evergreen cloud

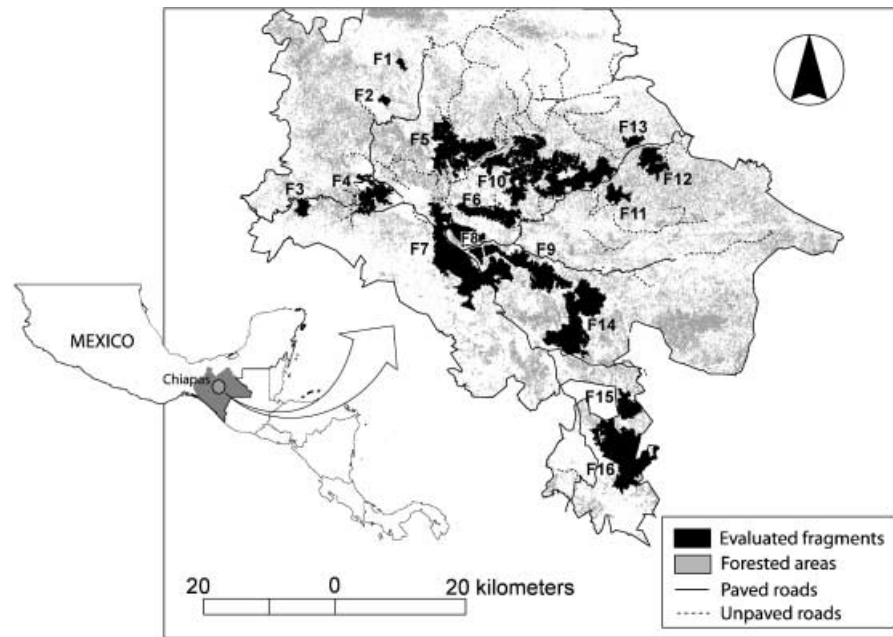


Fig. 1. The state of Chiapas in south-eastern Mexico and location of the studied forest fragments. The matrix surrounding forest fragments includes traditional shifting cropland, natural and induced pastureland and developed areas. Forest extent was based on land-cover classification of Enhanced Thematic Mapper (ETM+) Landsat imagery. Labels refer to fragment Id. in Table 1.

forests (Miranda 1952; Rzedowski 1978; Breedlove 1981; González-Espinosa *et al.* 1991). Traditional agricultural practices in this region have produced a landscape mosaic of forest fragments embedded in a matrix of secondary vegetation and crop fields (Ramírez-Marcial *et al.* 2001; Galindo-Jaimes *et al.* 2002). This mosaic landscape has many small patches of regenerating secondary forest and isolated trees. It may therefore be quite permeable for some tree species. However, deforestation in recent decades has reduced the connectivity of the landscape (Ochoa-Gaona & González-Espinosa 2000; Cayuela, Rey Benayas & Echeverría 2006). In particular, areas of mature vegetation with properties that permit the regeneration of late successional species appear to be becoming increasingly scarce and isolated.

TREE SPECIES DATA AND EXPLANATORY VARIABLES

We conducted inventories on 204 circular plots of 1000 m² in different forest fragments. Because field sampling took place prior to the acquisition of satellite images, it was impossible to define clear-cut boundaries for most of the fragments in our study. As a consequence, floristic inventories were rather unevenly distributed among fragments. In each plot, all trees with d.b.h. > 10 cm were identified to species and counted. The number of observed tree species per plot ranged between 2 and 28 and averaged 13.3 ± 5.2 . The number of stems per plot ranged between 22 and 211 and averaged 97.2 ± 36.5 . The final database included 230 native tree species. We used Fisher's alpha as a measure

of plot diversity. Fisher's alpha is a good estimator of α -diversity because it is independent of the number of individual trees in a sample (Rosenzweig 1995) and assumes an underlying parametric model for the distribution of species' abundances (Fisher, Corbet & Williams 1943).

To map the fragments, we classified a set of three Landsat Enhanced Thematic Mapper (ETM+) satellite images taken in April 2000 (path 21 row 48, path 21 row 49, path 22 row 48) with a resolution of 30×30 m. These images were geometrically, atmospherically and topographically corrected prior to classification (Cayuela, Golicher & Rey Benayas 2006). The study fragments were well distributed over the broader landscape and provided a valuable description of the regional diversity (Fig. 1). We discarded data collected from fragments with fewer than five plots in our analyses. This resulted in 195 plots allocated over 16 forest fragments (Table 1). The following fragment metrics were calculated: (i) area (ha); (ii) core area (area remaining after removing a buffer edge of 100 m) (ha); (iii) edge/area ratio [the ratio of the fragment perimeter (m) to area (m²)]; and (iv) mean proximity index (ratio between the size and proximity of all fragments whose edges were within 1 km of the focal fragment). These indices were computed by FRAGSTATS version 3.3 (McGarigal *et al.* 2002).

At the plot level, the set of explanatory variables included variables related to (i) climate, (ii) forest fragmentation and (iii) local human disturbance. (i) Climatic variables were generated for 1×1 -km cells using universal kriging (see details on sources of original data and their attributes in Golicher, Ramírez-Marcial & Levy-Tacher 2006). After analysing the redundancy

Table 1. Main features of the 16 forest fragments sampled in this study (Fig. 1). Core area is measured at a distance of 100 m to the fragment edge

Id	Number of plots	Observed species	Area (ha)	Core area (ha)
F1	10	54	71	15
F2	10	57	92	7
F3	9	49	269	17
F4	18	39	1195	340
F5	20	51	3032	656
F6	10	29	1182	303
F7	10	55	5664	2028
F8	5	30	209	66
F9	15	27	2207	623
F10	26	14	5282	299
F11	10	35	416	36
F12	10	38	880	101
F13	6	36	278	5
F14	18	44	3271	564
F15	7	12	721	120
F16	11	79	3382	614

in closely correlated variables, we reduced the 36 initial climatic variables to two variables, namely mean monthly rainfall and maximum temperature during the dry season (from January to May). (ii) The effects of fragmentation at this scale of analysis were measured as proximity to the nearest forest edge (m); this was divided by the maximum value in order to produce standardized values ranging between 0 and 1. (iii) Surrogates of human disturbance included canopy closure, measured as the proportion of forest cover in a 500-m radius circle centred on each plot (ranging between 0 and 1) and a degradation index (DI) ranging between -1 and 1 that was calculated as the relative change in the normalized difference vegetation index (NDVI) between 1990 Thematic Mapper (TM), 2000 ETM + Landsat satellite images, respectively:

$$DI = \frac{NDVI(2000) - NDVI(1990)}{NDVI(1990)}$$

Negative values of the degradation index indicated forest disturbance, for example by selective logging of certain species, whereas positive values indicated recent forest recovery.

DATA ANALYSES

We used ordination techniques to relate the variability in tree species composition to environmental gradients and to define major community types. We then tested the effects of forest fragmentation and local disturbance on tree species diversity within each of these community types. Effects manifested as differences between fragments were analysed by fitting simple linear models using the mean plot value of Fisher's alpha for each fragment (i.e. the fragment was the analytical unit). Effects within fragments were analysed by

looking at patterns in the deviations from the mean value for alpha within each fragment. To do this we used linear mixed-effects models. These models are appropriate for representing clustered, and therefore potentially correlated, data (Pinheiro & Bates 2000), as is the case for plots within separated fragments. They differ from the simple linear models in that they use plots as analytical units and assume that the effects at the fragment level are essentially random.

We also constructed species resampling curves for the different forest types in order to estimate how many species we would expect to lose for each forest type if the number of individuals in a fragment was halved. We assumed completely random associations between individuals and no selection for any particular species.

Community composition and environmental gradients

Canonical correspondence analysis (CCA) was used to identify key explanatory environmental variables of plot tree composition (see Appendix S1 in the supplementary material). Analysis of the eigenvalues for constrained as opposed to unconstrained axes suggested that imposing constraints did not produce an optimum arrangement of species and sites in ordination space. We therefore used the unconstrained technique of non-metric multidimensional scaling (NMDS) to look at the overall pattern of dispersion in species composition. We interpreted the ordination with respect to the major environmental variables identified in the CCA. NMDS was also used to group species and plots in order to identify major community types. Data were square-root transformed and then submitted to Wisconsin double standardization (Legendre & Gallagher 2001). We used the Bray-Curtis dissimilarity distance to compute the resemblance matrix among sites. Based on the NMDS plot, we generated smooth surfaces for the major climatic variables by fitting thin plate splines using general additive models and interpolating the fitted values on the unconstrained ordination diagram (Oksanen, Kindt & O'Hara 2005). CCA and NMDS were implemented by the R package 'vegan' (Oksanen, Kindt & O'Hara 2005).

Forest fragmentation, local disturbance and tree diversity

We used linear models to test statistically the effects of fragmentation *per se* on tree diversity. The fragment was used as the analytical unit and tree diversity was calculated as the mean of Fisher's alpha of all plots embedded within each fragment. The predictors of diversity used were area, core area, edge/area ratio and mean proximity index.

Linear mixed effects models were fitted for each of the community types previously defined in the ordination analyses. These models include fixed and random effects. The fixed effects were interpreted as within-fragment relationships, which occur over the set of

fragments making up each community type. These were proximity to edge, canopy closure and a degradation index. In addition, the intercept was modelled as a random effect. This effectively held for the variability at the fragment level by assuming that the mean values for Fisher's alpha were the results of random effects. These effects taken together were modelled as a Gaussian distribution.

All these analyses were also performed by guilds. Guilds grouped species, based on their requirements for exposure to the sun for healthy regeneration, into late successional and pioneer species (modified after Hill & Curran 2001). Categorization was based on the results of detailed observations of seedling populations in the studied forest mosaic (N. Ramírez-Marcial & M. Martínez Icó, personal communication) as well as on data from common garden experiments (A. Camacho-Cruz, L. Galindo-Jaimes, M. González-Espinosa, J.M. Rey Benayas & M.A. Zavala, unpublished data).

Predicting species loss

To investigate the potential effects of fragmentation and local disturbance on the loss of tree diversity, we constructed species resampling curves (Gotelli & Colwell 2001) under the *ceteris paribus* assumption (all things being equal) of island theory for the different forest fragments within each of the major NMDS community types. Rarefaction curves were used to avoid serial dependence between samples (O'Hara 2005). For 1000 resample sizes evenly spaced between 10% and 90% of the total number of individuals, s individuals were drawn from the sample without replacement and the number of species $S(s)$ in the subsample was counted. We calculated the number of species lost in each fragment by halving the number of individuals. We implemented the resampling technique using an R function described by O'Hara (2005).

Results

COMMUNITY COMPOSITION AND ENVIRONMENTAL GRADIENTS

Five major groups were defined according to the NMDS ordination, namely evergreen cloud forest, pine–oak–liquidambar forest, pine–oak forest, oak forest, and transitional forest (Table 2 and Fig. 2a). Floristic differences between these forest types were related to mean monthly rainfall and maximum temperature during the dry season (Fig. 2b). This was supported by analyses of the variance (mean monthly rainfall, $F_{4,193} = 113.7$, $P < 0.0001$; maximum temperature during the dry season, $F_{4,193} = 67.2$, $P < 0.0001$).

EFFECTS OF FOREST FRAGMENTATION AND LOCAL DISTURBANCE ON TREE DIVERSITY

At the fragment level, there was no significant correlation between mean Fisher's alpha and fragment size ($r = -0.11$, $P = 0.680$), core area ($r = -0.11$, $P = 0.672$), edge/area ratio ($r = -0.12$, $P = 0.664$) and mean proximity index ($r = -0.41$, $P = 0.120$). The results were also non-significant for late successional and pioneer species (results not shown).

The five forest communities differed in alpha tree diversity (ANOVA $F_{4,193} = 35.42$, $P < 0.0001$; Fig. 3). We explored in detail the effects of fragmentation and local disturbance within fragments in those groups for which there were more than one fragment, namely evergreen cloud forest, pine–oak–liquidambar forest and pine–oak forest. Linear mixed-effects models revealed notable differences in diversity between fragments (random effects) for evergreen cloud and pine–oak–liquidambar forests (Table 3). There was also considerable variation in alpha diversity that was not linked to the random effect but to variables related to fragmentation and

Table 2. Summary of main environmental features and tree species that characterize the different forest types as resulting from interpretation of NMDS ordination. Nomenclature of species follows Breedlove (1986) and N. Ramírez-Marcial (personal communication)

Forest type	Environmental features	Characteristic species
Evergreen cloud	Altitude between 2000 and 2700 m. Permanent humid conditions as a result of high rainfall and/or fog interception	<i>Persea americana</i> , <i>Clethra macrophylla</i> , <i>Cleyera theoides</i> , <i>Prunus brachybotrya</i> , <i>Parathesis leptopa</i> , the arborescent fern <i>Cyathea fulva</i>
Pine–oak–liquidambar	Altitude between 1800 and 2100 m, high rainfall and low seasonality	<i>Quercus crispipilis</i> , <i>Pinus oocarpa</i> , <i>Liquidambar styraciflua</i> , <i>Clethra suaveolens</i> , <i>Rapanea myricoides</i> , <i>Saurauia scabrida</i>
Pine–oak	Altitude between 2100 and 2600 m, exposed to highly seasonal conditions	<i>Quercus crassifolia</i> , <i>Quercus laurina</i> , <i>Quercus rugosa</i> , <i>Pinus ayacahuite</i> , <i>Pinus pseudostrobus</i> , <i>Pinus tecunumanii</i> , <i>Garrya laurifolia</i> , <i>Arbutus xalapensis</i> , <i>Alnus acuminata</i> , <i>Cornus disciflora</i> , <i>Oreopanax xalapensis</i> , <i>Prunus serotina</i> , <i>Rapanea juergensenii</i>
Oak	Altitude between 1900 and 2100 m, dry climatic conditions	<i>Quercus segoviensis</i> , <i>Juniperus gamboana</i>
Transitional	Altitude below 1700 m, warm temperatures and dry climatic conditions	<i>Ternstroemia oocarpa</i> , <i>Sebastiania cruenta</i> , <i>Eugenia capulioides</i> , <i>Parathesis belizensis</i> , <i>Xylosma flexuosum</i> , <i>Cupania dentata</i>

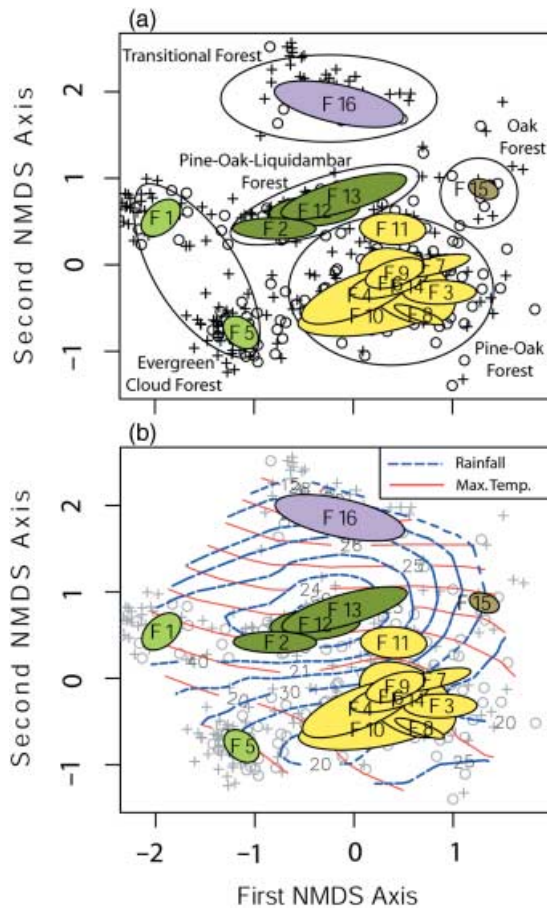


Fig. 2. Non-metric multidimensional scaling ordination of tree species composition (circles, sites; crosses, species) in 204 plots showing (a) the identification of community types and (b) the interpretation of the ordination axes with respect to major climatic variables. Labels refer to fragment Id in Table 1.

local disturbance (Fig. 4). Canopy closure was, in all cases, highly correlated with the intercept ($r > 0.8$), suggesting that this variable might be important in determining differences in diversity between fragments in addition to within fragments. For the two remaining forest types (oak and transitional forests), simple regressions resulted in non-significant relationships between tree diversity and the variables related to fragmentation and local disturbance (results not shown).

An analysis by guilds revealed that effects were most noticeable for late successional species rather than pioneer species (Table 3 and Fig. 4). This was particularly relevant in pine–oak and pine–oak–liquidambar forests, where no significant relationships between alpha diversity of pioneer species and any of the variables related to fragmentation and local disturbance were found.

PREDICTING SPECIES LOSS

One model for species loss assumes that smaller fragments hold fewer individuals. This assumption did not strictly apply to our studied fragments (Fig. 5). Thus the island biogeography hypothesis in its simplest form has to be investigated by random resampling from the collection of individuals for each fragment (rarefaction). A large number of randomly drawn samples of individuals of varying sizes was drawn from the sample of individuals from each fragment within each community type and the estimated number of species was plotted against the logarithm of the number of individuals. Visual analysis and a plot of the residuals suggested that a straight line relationship was appropriate in all 16 fragments (results not shown). The slope of these

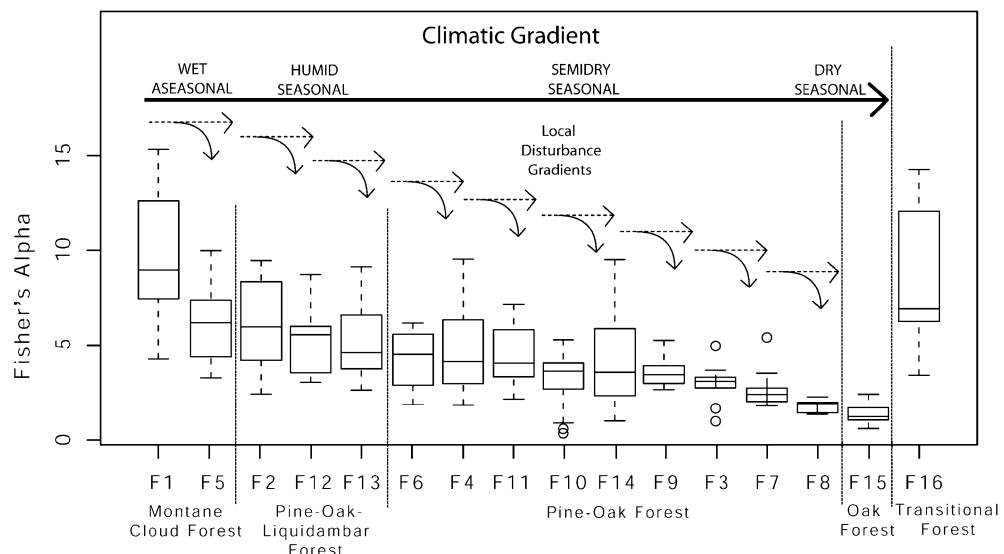


Fig. 3. Box-plots of alpha tree diversity for each forest fragment grouped by forest type and ordered according to median value. The figure includes the authors' interpretation of the result with relation to regional climatic and local disturbance gradients.

Table 3. Fixed effects terms of linear mixed-effects models for evergreen cloud forest, pine–oak–liquidambar forest and pine–oak forest considering all tree species (left column), late successional species (central column) and pioneer species (right column). Plots grouped within fragments are assumed to be correlated; thus the models treat the intercept for each fragment as a random effect. Values of $P < 0.05$ are shown in bold

Forest type	Explanatory variable	All species				Late successional				Pioneer			
		Value	SE	d.f.	P	Value	SE	d.f.	P	Value	SE	d.f.	P
Evergreen cloud	Intercept	17.07	4.27	25	< 0.001	16.94	3.51	25	< 0.001	-3.19	3.00	25	0.298
	Proximity to edge	-10.9	4.42	25	0.021	-6.54	3.84	25	0.101	-5.82	1.72	25	0.002
	Canopy closure	-9.85	5.06	25	0.063	-11.77	4.08	25	0.008	7.43	3.64	25	0.052
	Degradation index	7.46	6.07	25	0.231	3.32	5.26	25	0.534	3.97	2.41	25	0.111
Pine–oak–liquidambar	Intercept	7.94	2.32	20	0.003	3.18	1.36	20	0.030	4.95	2.08	20	0.027
	Proximity to edge	3.24	4.44	20	0.474	-1.42	2.60	20	0.589	5.80	3.98	20	0.161
	Canopy closure	-4.45	4.36	20	0.319	0.37	2.55	20	0.886	-4.36	3.90	20	0.277
	Degradation index	5.85	3.24	20	0.086	5.11	1.89	20	0.014	1.64	2.90	20	0.579
Pine–oak	Intercept	1.54	1.05	109	0.145	-0.02	1.16	109	0.986	-1.73	0.61	109	0.005
	Proximity to edge	-2.41	1.06	109	0.026	-3.08	1.17	109	0.010	-0.08	0.59	109	0.892
	Canopy closure	3.75	1.44	109	0.011	3.31	1.60	109	0.041	0.86	0.82	109	0.297
	Degradation index	2.43	1.20	109	0.045	2.70	1.32	109	0.043	0.27	0.66	109	0.682

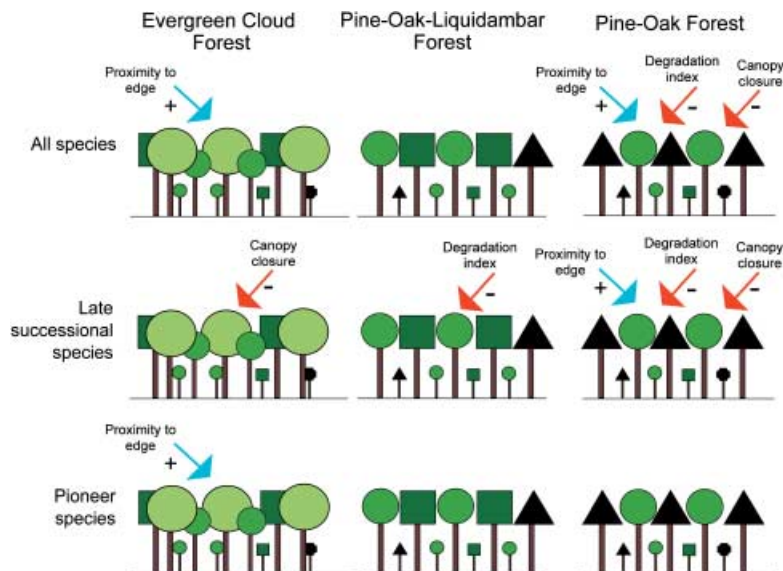


Fig. 4. Representation of within-fragment effects (fixed effects) of fragmentation and local disturbance on tree diversity for evergreen cloud forest, pine–oak–liquidambar forest and pine–oak forest considering all tree species (upper), late successional species (middle) and pioneer species (bottom).

lines and the values of Fisher’s alpha are shown in Table 4. Theory indicates that if the species’ abundance relationship in a sample follows a log series, then Fisher’s alpha will equal this slope. This assumption was found to be true in most cases, and provided strong justification for using Fisher’s alpha as the preferred diversity index for further analysis. The approximate number of species that would be lost when fragment size was halved ranges between 5% and 21% (Table 4). The maximum loss of species was predicted to occur in the transitional zone between pine–oak and lowland tropical deciduous forests (12 species lost) and the highly diverse evergreen cloud forest fragments (seven to nine species lost); the minimum predicted was associated to oak forest fragments (three species lost).

Discussion

The results of the analyses performed at the fragment level suggest that the effects of fragmentation *per se* on tree diversity are not directly observable. Given the slow response of tree populations to isolation of the remnant fragments, it is likely that the full impact of these changes will not become apparent for some time (Hanski & Ovaskainen 2002; Helm, Hanski & Pärtel 2006). Lack of detection does not necessarily mean that these effects are not important. Rather it indicates statistical and conceptual model limitations. One of these limitations is related to the scale at which interactions of species with their environment take place. Cushman & McGarigal (2004) suggested that bird species interact most strongly with fine-scale habitat, within the

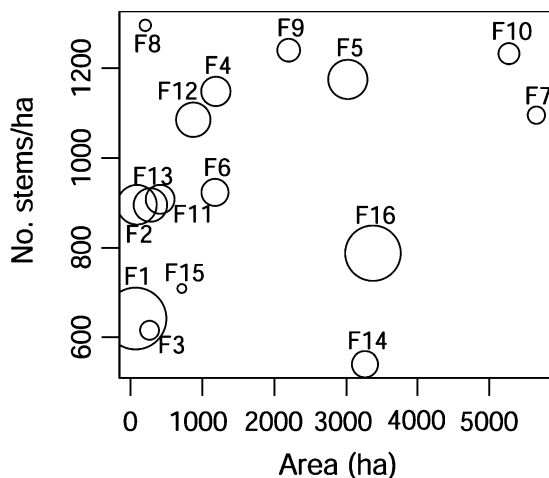


Fig. 5. Relationship between the number of trees and the size of the forest fragment (ha) ($r = 0.27$, $P = 0.30$). The size of the data points represents mean plot values of Fisher's alpha.

range of their immediate perception. This is the scale at which predation, competition and other interspecific interactions occur, and at which the organisms experience their environment (Levey *et al.* 2005). As a consequence, the fragment scale might not be appropriate for detecting the impacts of fragmentation and local disturbance. Our results support this hypothesis for tree diversity. We found that fragmentation and disturbance act simultaneously on tree diversity at a local scale, yet with opposite effects. Edge effects had a weak but positive effect on tree diversity, whereas local disturbance was negatively related to it.

In a recent study based on a review of 17 empirical studies ranging from small-scale experimental studies to continental-scale analyses, Fahrig (2003) pointed out that the effects of fragmentation on diversity were ambiguous and as likely to be positive as negative. Apparently contradictory results are based on studies that differ in the spatial and temporal scale, degree of environmental variability (which is often not considered), history of human use, targeted organisms and response variable (presence/absence, abundance, different diversity indices, etc.). In our study, we could not detect the effects of fragmentation at the fragment level, but we did find that edges had a positive effect on tree diversity at the plot level. This might be because, in the Highlands of Chiapas, many land-use practices leading to habitat modification do not create barriers to the species, as opposed to the traditional concept of fragmentation which implies that high-quality habitat remnants are isolated by a hostile environment to the organisms that thrive in the remnants. This is also the case in other mountainous tropical regions of Central and South America, where traditional shifting cultivation land use has created a matrix still dominated by semi-natural vegetation in various states of modification (Kappelle 2006). Under these circumstances, forest edges do not become hard boundaries between contrasting habitats but allow many species to disperse

Table 4. Fisher's alpha and slope of the resampled species accumulation curves. Assuming random placement the model has been used to predict the number and percentage of tree species that would be lost by halving the number of individuals in each fragment within each forest type

Forest type	Fragment	Fisher's alpha	Log (slope)	Species lost	
				<i>n</i>	%
Evergreen	F1	14.1	12.5	8.6	15.9
	F5	10.5	10.5	7.3	12.8
Pine-oak-liquidambar	F2	11.1	8.9	6.2	12.6
	F12	11.1	10.1	7.0	13.7
Pine-oak	F13	8.7	8.1	5.6	15.5
	F3	6.5	8.5	5.9	20.3
	F4	10.4	7.9	5.5	10.0
	F6	5.9	4.5	3.1	10.3
	F7	5.0	5.5	3.8	16.4
	F8	2.5	1.8	1.3	9.3
Oak	F9	6.1	4.9	3.6	10.3
	F10	6.1	2.7	1.9	5.0
	F11	8.3	8.2	5.7	14.6
Transitional	F14	9.5	9.3	6.5	14.8
	F15	2.2	3.6	2.5	20.8
	F16	21.1	17.3	12.0	15.2

and flourish (Laurance *et al.* 1998; Laurance & Cochrane 2001; López-Barrera & Newton 2005; López-Barrera *et al.* 2006). Consequently, tree diversity increases near the forest edges (Table 3 and Fig. 4). This increase might occur as the result of an increase of the more opportunistic pioneer species near the forest edges (Laurance *et al.* 1998; Metzger 2000; Hill & Curran 2001; Kupfer, Webbeking & Franklin 2004). However, we found that the positive effect of forest edges on tree diversity affected both the pioneer and late successional species. The reason for this might be related to the time lag of tree species colonization (Helm, Hanski & Pärtel 2006). After a gap is opened in the forest, pioneer species tend to colonize the forest edge. Late successional species have a lower chance of colonizing these sites but mature trees growing near the forest edge can persist. Consequently these effects are likely to be neglected in the short term. Furthermore, categorization of species by dispersal traits (dispersal distance, agents of dispersal, etc.) and/or age ranges (e.g. by measuring saplings vs. trees) might lead to differential sensitivities to fragmentation (Henle *et al.* 2004). At present, this information does not exist for the flora of our study area.

Human disturbance is typically considered to have a negative effect on biodiversity. Even so, clearer definitions of what is implied by changes in species composition are needed. Humans are capable of subtle manipulations (e.g. harvesting particular size classes of a specific species). Thus it can be difficult to know how much the correlates we found reflect controlling forces, and what the unmeasured role of humans might be. In addition, intense disturbance regimes may lead to a loss of biodiversity by triggering secondary succession (Fig. 3). Oak *Quercus* species and other broad-leaved species are preferentially logged. Under intense disturbance

regimes there is a tendency for early successional stages to be dominated by pine *Pinus* species, particularly in drier areas (González-Espinosa *et al.* 1991; Ramírez-Marcial *et al.* 2001; Galindo-Jaimes *et al.* 2002). But if no disturbance occurs, oak and broad-leaved species tend to replace pines upon their death. This successional gradient related to traditional land use is complex (González-Espinosa, Ramírez-Marcial & Galindo-Jaimes 2006). The transitional forest found between pine–oak and lowland tropical deciduous forests seems to harbour higher tree diversity, perhaps as a result of biogeographical factors acting at a broader scale.

A limitation of this study is that our data represent a ‘snapshot’ in the dynamic process of fragmentation. This makes it difficult to understand where we stand and on what trajectory in such a dynamic process. Further investigations on the regional patterns of tree diversity and local human disturbance are needed in order to clarify these relationships. Our findings support the hypothesis that many tree species have the capacity to overcome the problems posed by fragmented landscapes in the short term. This study also emphasizes the need to choose appropriate analytical tools to evaluate the effects of fragmentation and local disturbance at different spatial scales. We conclude that in the studied forests (i) plot-level variation was more important in structuring plant communities than fragment-level variation, (ii) fragmentation and local disturbance acted simultaneously on tree diversity at the plot level, and (iii) local habitat disturbance had a higher detrimental impact on diversity than habitat fragmentation, particularly for late successional tree species. These conclusions do not contradict the theory of island biogeography. Rather, they suggest that a simple underlying theory is not sufficient to describe the complex processes acting in terrestrial systems or predict either their short- or long-term effects.

As a consequence of these findings we suggest that conservation initiatives aimed at retaining tree diversity within each of the major forest types should focus on mitigating the immediate effects of local disturbance. It is particularly important to protect as many of the remaining areas of mature native forests as possible. These are usually found within a matrix of forest of lower conservation value. They are small in size and widely dispersed across the landscape (Cayuela, Golicher & Rey-Benayas 2006). Increasing the effective size of these high-value areas by maintaining forest buffer zones would also have a positive effect on tree diversity. This would be particularly valuable if combined with active enrichment with late successional tree species in order to accelerate succession (Martínez-Garza & Howe 2003). The area of protected forest alone does not provide an indicator of the effectiveness of conservation if not combined with a measure of forest quality.

Priorities for conservation should not be based on landscape-scale metrics alone. This point is particularly important in the context of a growing reliance in the conservation community on remotely sensed data

that does not (as yet) allow direct measurements of diversity. Loss of connectivity and reduction in fragment size can potentially be reversed through restoration measures. However, if the present widespread loss of internal forest quality is allowed to take place, it will become permanent.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from <http://www.blackwell-synergy.com>.

Appendix I. Canonical Correspondence Analysis and environmental gradients